SOME EFFECTS OF A UNIQUE HYDROELECTRIC DEVELOPMENT ON THE LITTORAL BENTHIC COMMUNITY AND ECOLOGY OF TROUT IN A LARGE NEW ZEALAND LAKE

BY

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ABSTRACT

A three year study (1974-1977) examined the effects of hydroelectric development on the littoral invertebrate fauna and ecology of brown trout (*Salmo trutta* L.) and rainbow trout (*Salmo gairdneri* Richardson) in Lake Waikaremoana on the North Island of New Zealand.

Lake Waikaremoana was formed over 2000 years ago by a massive landslide, which created a natural rock and earth-fill dam. Its development for hydroelectric purposes in 1946 was unique in that the lake level was initially lowered rather than being raised.

The most significant morphometric changes following hydroelectric development were a disproportionately great loss of littoral area, and the creation of deep winding channels at the stream mouths entering the lake.

In recent years the amplitude of lake level fluctuations has not been significantly greater than the amplitude of the natural lake level fluctuations, but their seasonal periodicity has been reversed. The seasonal changes in the depth distribution of the littoral invertebrate fauna are adapted to a falling lake level in summer and a rising lake level in winter. Hydroelectric drawdown is now concurrent with an upward migration of some animals during winter. The maximum density of animals in the deep littoral in summer no longer coincides with a falling lake level and increasing light penetration, but instead is subjected to deeper submergence and reduced
water transparency due to summer storage of water.

The small juvenile and large, old trout are most dependent on the shallow littoral space, and there is an increasing utilization of the littoral food resources with increasing age and size. The combined effects of the morphometric changes and unnatural fluctuations in lake level, through reduction of littoral space and food resources, has decreased the carrying capacity of the lake for trout to a degree out of proportion to the overall reduction in the surface area of the lake.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>ii</td>
</tr>
<tr>
<td>Table of Contents</td>
<td>iv</td>
</tr>
<tr>
<td>List of Tables</td>
<td>vii</td>
</tr>
<tr>
<td>List of Figures</td>
<td>viii</td>
</tr>
<tr>
<td>Acknowledgements</td>
<td>x</td>
</tr>
<tr>
<td><strong>I. INTRODUCTION</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>II. STUDY AREA</strong></td>
<td>4</td>
</tr>
<tr>
<td>A. LAKE WAIKAREMOANA AND CATCHMENT</td>
<td>4</td>
</tr>
<tr>
<td>Geographical location and geology</td>
<td>4</td>
</tr>
<tr>
<td>Lake formation</td>
<td>6</td>
</tr>
<tr>
<td>The catchment</td>
<td>7</td>
</tr>
<tr>
<td>Native fish and introduced species</td>
<td>9</td>
</tr>
<tr>
<td>B. HYDROELECTRIC DEVELOPMENT</td>
<td>10</td>
</tr>
<tr>
<td>C. LAKE LEVEL FLUCTUATIONS</td>
<td>13</td>
</tr>
<tr>
<td>Amplitude</td>
<td>13</td>
</tr>
<tr>
<td>Seasonal periodicity</td>
<td>15</td>
</tr>
<tr>
<td>Major cycle</td>
<td>18</td>
</tr>
<tr>
<td>Rate of rise and fall</td>
<td>18</td>
</tr>
<tr>
<td><strong>III. MATERIALS AND METHODS</strong></td>
<td>20</td>
</tr>
<tr>
<td>A. PHYSICAL</td>
<td>20</td>
</tr>
<tr>
<td>Surveys of the lake shore</td>
<td>20</td>
</tr>
<tr>
<td>Planimetry</td>
<td>21</td>
</tr>
<tr>
<td>Water transparency and temperature</td>
<td>22</td>
</tr>
<tr>
<td>Lake level, power generation and rainfall</td>
<td>23</td>
</tr>
</tbody>
</table>
B. LITTORAL BENTHOS ....................................... 23
   Ekman dredge sampling ................................. 23
   Statistical procedure .................................. 27
C. ZOOPLANKTON AND LARVAL FISH ......................... 27
D. TROUT .................................................... 29
   Netting programme ..................................... 29
   Stomach analysis ....................................... 31

IV. RESULTS .................................................. 32
A. PHYSICAL ................................................ 32
   Morphometric changes .................................. 32
   Thermal conditions and water transparency .......... 34
   Dissolved oxygen ...................................... 36
B. AQUATIC MACROPHYTES ................................. 36
C. LITTORAL BENTHOS ....................................... 39
   Sampling variability .................................. 39
   Depth distribution .................................... 43
   Composition .......................................... 45
   Seasonal changes in depth distribution .............. 48
   Molluscs ............................................... 52
   Odonata and Lepidoptera .............................. 52
   Trichoptera ........................................... 56
   Chironomids ........................................... 58
D. TROUT .................................................... 58
   Composition of the total catch ....................... 58
   Spatial distribution .................................. 60
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stomach analysis</td>
<td>63</td>
</tr>
<tr>
<td>Limnetic food resources</td>
<td>66</td>
</tr>
<tr>
<td>Recruitment of juveniles to lake</td>
<td>68</td>
</tr>
<tr>
<td>Condition factor</td>
<td>69</td>
</tr>
<tr>
<td><strong>V. DISCUSSION</strong></td>
<td>73</td>
</tr>
<tr>
<td>A. MORPHOMETRIC CHANGES</td>
<td>73</td>
</tr>
<tr>
<td>B. LAKE LEVEL FLUCTUATIONS</td>
<td>74</td>
</tr>
<tr>
<td>Seasonal periodicity</td>
<td>74</td>
</tr>
<tr>
<td>Effects on light penetration and primary producers</td>
<td>78</td>
</tr>
<tr>
<td>Major cycle</td>
<td>80</td>
</tr>
<tr>
<td>Rate of rise and fall</td>
<td>81</td>
</tr>
<tr>
<td>C. LITTORAL INVERTEBRATE FAUNA</td>
<td>82</td>
</tr>
<tr>
<td>Quantitative losses</td>
<td>84</td>
</tr>
<tr>
<td>Seasonal changes in depth distribution</td>
<td>85</td>
</tr>
<tr>
<td>Qualitative losses</td>
<td>88</td>
</tr>
<tr>
<td>D. TROUT</td>
<td>89</td>
</tr>
<tr>
<td>Species composition</td>
<td>89</td>
</tr>
<tr>
<td>Spatial segregation</td>
<td>90</td>
</tr>
<tr>
<td>Effects of hydroelectric development on available space</td>
<td>93</td>
</tr>
<tr>
<td>Food and condition factor</td>
<td>94</td>
</tr>
<tr>
<td>Effects of hydroelectric development on food resources</td>
<td>95</td>
</tr>
<tr>
<td>VI. SUMMARY</td>
<td>97</td>
</tr>
<tr>
<td>VII. MANAGEMENT IMPLICATIONS</td>
<td>99</td>
</tr>
<tr>
<td>VIII. LITERATURE CITED</td>
<td>100</td>
</tr>
</tbody>
</table>
LIST OF TABLES

<table>
<thead>
<tr>
<th>TABLE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. The Morphometry of Lake Waikaremoana (at lake level 608 metres a.s.l.)</td>
<td>8</td>
</tr>
<tr>
<td>II. The seasonal periodicity of lake level fluctuations before and after hydroelectric development</td>
<td>17</td>
</tr>
<tr>
<td>III. Morphometric changes in Lake Waikaremoana following hydroelectric development of the lake</td>
<td>33</td>
</tr>
<tr>
<td>IV. Sampling variability within the drawdown (at 2-3m), mixed (at 5-6m), and Nitella (at 11-12m) zones at Hautaruke Bay</td>
<td>40</td>
</tr>
</tbody>
</table>
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Lake Waikaremoana and catchment showing the inflowing streams</td>
<td>5</td>
</tr>
<tr>
<td>2. The outlet of Lake Waikaremoana before and after hydroelectric development</td>
<td>12</td>
</tr>
<tr>
<td>3. Lake level fluctuations in Lake Waikaremoana from 1931 - 1976. From data provided by the New Zealand Electricity Department</td>
<td>14</td>
</tr>
<tr>
<td>4. The periodicity of lake level fluctuations in Lake Waikaremoana before and after hydroelectric development. Mean monthly rainfall (Onepoto) and mean monthly power generation (Kaitawa)</td>
<td>16</td>
</tr>
<tr>
<td>5. Lake level fluctuations in Lake Waikaremoana, and six monthly rainfall (Onepoto) and power generation (Kaitawa) 1961-1976</td>
<td>19</td>
</tr>
<tr>
<td>6. Lake Waikaremoana showing shoreline geology, lost littoral, bathymetry and station locations</td>
<td>25</td>
</tr>
<tr>
<td>7. Diagrammatic transects of a) the littoral zone at Hautaruke Bay - benthos sampling station and b) the netting stations showing the positioning of the gillnets</td>
<td>26</td>
</tr>
<tr>
<td>8. The net used for sampling larval fish</td>
<td>28</td>
</tr>
<tr>
<td>10. The temperature and dissolved oxygen profiles in Lake Waikaremoana towards the end of the period of thermal stratification 1975</td>
<td>37</td>
</tr>
<tr>
<td>11. The depth distribution of total animals, molluscs, insects and oligochaetes in the littoral zone at Hautaruke Bay</td>
<td>44</td>
</tr>
<tr>
<td>12. The composition of the littoral invertebrate fauna at Hautaruke Bay</td>
<td>46</td>
</tr>
<tr>
<td>13. Seasonal changes in the depth distribution of total animals at Hautaruke Bay</td>
<td>49</td>
</tr>
<tr>
<td>Figure</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>------</td>
</tr>
<tr>
<td>14. Seasonal changes in the depth distribution of molluscs, insects and oligochaetes at Hautaruke Bay</td>
<td>51</td>
</tr>
<tr>
<td>15. Seasonal changes in the depth distribution of gastropods and bivalves at Hautaruke Bay</td>
<td>53</td>
</tr>
<tr>
<td>16. Seasonal changes in the depth distribution of Odonata and Lepidoptera at Hautaruke Bay</td>
<td>55</td>
</tr>
<tr>
<td>17. Seasonal changes in the depth distribution of Trichoptera at Hautaruke Bay</td>
<td>57</td>
</tr>
<tr>
<td>18. Seasonal changes in the depth distribution of chironomids at Hautaruke Bay</td>
<td>59</td>
</tr>
<tr>
<td>19. The composition of the total catch of trout in the gillnets from both stations, according to species, size and maturity</td>
<td>61</td>
</tr>
<tr>
<td>20. The length frequency distributions of trout caught in gillnets in the drawdown zone, in the deep littoral zone and in the limnetic zone, from both stations</td>
<td>62</td>
</tr>
<tr>
<td>21. The composition of the diets of brown and rainbow trout in Lake Waikaremoana</td>
<td>65</td>
</tr>
<tr>
<td>22. Seasonal changes in the size and numbers of larval smelt and larval bullies, and in the numbers of Daphnia in Lake Waikaremoana</td>
<td>67</td>
</tr>
<tr>
<td>23. The length frequency distributions of rainbow trout caught in gillnets during each 2-monthly sampling (October 1975 - February 1976)</td>
<td>70</td>
</tr>
<tr>
<td>24. The mean condition factor of rainbow trout in relation to size and maturity</td>
<td>71</td>
</tr>
<tr>
<td>25. The seasonal periodicity and amplitude of the natural fluctuations in lake level in a) Lake Blåsjön, northern Sweden b) Loch Lomond, Scotland and c) Lake Waikaremoana</td>
<td>75</td>
</tr>
<tr>
<td>26. The natural and regulated lake level fluctuations in Lake Blåsjön and Lake Waikaremoana</td>
<td>77</td>
</tr>
<tr>
<td>27. The depth distribution of the bottom fauna in Lakes Blåsjön and Ankarvattnet, and in Lake Waikaremoana</td>
<td>83</td>
</tr>
</tbody>
</table>
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INTRODUCTION

The development of a lake for hydroelectric power generation usually involves the construction of a dam, and raising of the lake level with flooding of the low-lying surrounding land. But, in the case of Lake Waikaremoana, the construction of a dam was not required. The Lake had been formed by a natural rock and earth-fill dam as a result of a massive landside, which occurred over 2000 years ago. Its development for hydroelectric purposes in 1946 was unique in that the lake level was initially lowered rather than being raised.

In temperate regions lakes usually pass through three recognized stages following hydroelectric development (Rzoska 1966). The first of these stages - the "damming-up effect" - is frequently associated with increased planktonic production (Axelsson 1961, Rodhe 1964) and increased growth rates of fish (Runnström 1951, Frost 1956, Campbell 1963). This has in part been attributed to the release of nutrients from submerged terrestrial vegetation and soil (Rawson, 1958), the increase in space and consequent reduction in the population density of fish (Elder 1965) and the availability to bottom-feeding fish of submerged terrestrial invertebrates (Campbell 1963, Nilsson 1964). But the first stage is usually only transitory, lasting at best 2-5 years (Campbell 1957, Stube 1958, Rzoska 1966). It is followed by the second stage - a general depression in productivity - during which the inorganic
sediments underlying the soils of the inundated land are eroded and the new littoral zones are unstable (Grimás 1965). This produces an avalanche effect of inorganic sediments into the deeper littoral and profundal zones (Lindström 1973).

As the new littoral zones physically stabilize the lake passes into the third stage - a gradual recovery in productivity. Organic sediments start to build up in the profundal zone, and depending upon the extent and regime of lake level fluctuations, rooted aquatic macrophytes may recover to some extent in the littoral zones. However, these hydroelectric lakes seldom regain their former productivity (Rawson 1958, Rzoska 1966, Lindström 1973).

In southern Russian reservoirs the onset of this recovery may occur after a 6-10 year period of depression, and at higher latitudes (>50°N) recovery may be delayed for up to 25-30 years (Beckman 1966).

Lake Waikaremoana did not experience a "damming-up effect" immediately following hydroelectric development. It probably entered directly into a depression stage, but by now (some 30 years later) should be well into the "third stage" of gradual recovery. The initial deterioration in the trout fishery gave rise to increasing pressure from regional angling clubs on the fisheries management authorities to take remedial action. This pressure was frequently in the form of demands for the liberation of large numbers of hatchery-reared trout. The futility of stocking thousands of fry or fingerlings in such
hydroelectric lakes is discussed by Elder (1965). The New Zealand Wildlife Service, who are responsible for the management of Lake Waikaremoana, wisely resisted these demands and instead instigated a 3 year study (made possible by a grant from the New Zealand Electricity Department), which was carried out between August 1974 and August 1977. The purpose of this study was to gain a better understanding of the trout fishery of Lake Waikaremoana and the impacts of hydroelectric development. Some of the findings form the basis of this thesis.

Particular attention was paid to

1. The morphometric changes resulting from the lowering of the lake level, and

2. The altered seasonal periodicity of the lake level fluctuations in relation to the seasonal changes in the depth distribution of the littoral invertebrate fauna, and the distribution and feeding ecology of the trout.

Unfortunately, as with most such studies (Geen 1974), there was little available data on the ecology of trout or the limnology of Lake Waikaremoana from the period before hydroelectric development. This problem was overcome to some degree by Grimås (1961) in his studies of the hydroelectric-regulated Lake Blåsjö in northern Sweden by using a similar, nearby, undeveloped lake (Lake Ankarvattnet) as a "before" study. This approach was considered for the Lake Waikaremoana study, but although there is a smaller undeveloped lake within its catchment (Lake Waikareiti) the dissimilarities were too
great to use this lake for comparative ("before") studies. Conclusions regarding the ecological significance of the im-
pacts of hydroelectric development on Lake Waikaremoana are therefore somewhat speculative in nature.

STUDY AREA
LAKE WAIKAREMOANA AND CATCHMENT
Geographical location & geology

Lake Waikaremoana, with a maximum depth of 248 metres and a surface area of 51 square kilometres, is the deepest, but not the largest lake on the North Island of New Zealand. The lake lies at an elevation of 610 metres above sea level in the Urewera Mountains, at Latitude 38° 45'S and Longitude 177° 05'E (Figure 1). This area of the North Island of New Zealand lies directly over the plate margins of the Pacific and Australian plates, a tectonically active subduction zone with moderately frequent earthquakes and an active volcanic belt ≈ 100 kms. to the west. Convergence of the plates is taking place at a rate of 3-7 cms. a year (Minster et al 1974).

The shoreline and basin of the lake are composed of Terti-
ary sedimentary rocks, 10-22 million years old (N.Z. Geol. Survey). They consist of alternating strata of sandstone and a soft, light grey-coloured siltstone (papa). These alternating strata vary from a few centimetres thick to over 30 metres thick. They are tilted, dipping at an angle of about 18° in a southeasterly direction (Carter 1951). In the northwest
FIGURE 1. Lake Waikaremoana and catchment showing the inflowing streams. Bars across the larger streams indicate the location of waterfalls impassable to upstream migrating trout.
corner of the catchment the rocks are older, with outcroppings of Jurassic greywacke in the Hopuruahine catchment (N.Z. Geological Survey). An overlay of pumice (approximately 3 metres thick) blankets the sedimentary rocks throughout much of the catchment.

Lake formation

Lake Waikaremoana was formed by a landslide, which broke off the Ngamoko Range (Figure 1) and slumped down against the Panekiri bluffs obliterating a deep narrow gorge, through which the old Waikare-Taheke River had previously flowed, thus creating a massive natural rock and earth-fill dam (Anderson 1948). This damming back of the Waikare-Taheke River created a lake similar in morphometry to the much more recent man-made hydroelectric river-reservoirs, although the dam has a much more gradual slope into the lake than the man-made variety.

The forested valleys, which were flooded, now form the lake basin, and many of the trees of this drowned forest persist to this day as standing stumps in the lake-bed. It was through radioactive carbon dating of this drowned forest that the lake's age was determined - approximately 2200 years (Dr. V.H. Jolly pers.comm.).

The outflow was largely through subsurface leaks in the natural dam (Figure 2), and only occasionally did the lake level rise sufficiently to form a surface overflow (Figure 3). For this reason the lake level remained either relatively
stable, or else had been rising only very gradually since the lake was formed, allowing wave erosion to work persistently on the shores over a restricted vertical range. The wave-cut terraces, which were carved from the open papa shores, and the deltas, which were built at the numerous stream mouths entering the lake, remained submerged, and considerably increased the area of shallow littoral in this deep, steep-sided lake. A continuous surface overflow would have caused rapid erosion and cutting down of the lip of the dam, with a consequent progressive lowering of the lake level and "loss" of these shallow littoral areas (as occurs in most lakes). Some of the present morphometric characteristics are given in Table 1.

The catchment

The catchment of Lake Waikaremoana, which is about 7 times the area of the lake, consists almost entirely of undisturbed beech forest and forms a small part of the Urewera National Park. The mean annual rainfall is about 200-250 cms.

Highway 38 passes through the catchment from the outlet along the eastern shores of the lake to the northern corner of the catchment. At Home Bay (Figure 1) and nearby at Aniwaniwa there are situated a tourist complex and the Park Headquarters respectively. These are the only permanent human settlements within the catchment. Trampers, fishermen, hunters and others visit the lake throughout the year, and up to 500-1000 visitors per day stay at these two locations during peak holiday
Table 1. The Morphometry of Lake Waikaremoana (at lake level 608 metres a.s.l.).

<table>
<thead>
<tr>
<th>Characteristic</th>
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</tr>
</thead>
<tbody>
<tr>
<td>AREA OF CATCHMENT:</td>
<td>371 square kilometres</td>
</tr>
<tr>
<td>AREA OF LAKE:</td>
<td>51.4 square kilometres</td>
</tr>
<tr>
<td>LENGTH OF SHORELINE:</td>
<td>93.2 kilometres</td>
</tr>
<tr>
<td>SHORELINE DEVELOPMENT:</td>
<td>3.67</td>
</tr>
<tr>
<td>VOLUME OF LAKE:</td>
<td>$4.76 \times 10^9$ cubic metres</td>
</tr>
<tr>
<td>MAXIMUM DEPTH:</td>
<td>248 metres</td>
</tr>
<tr>
<td>MEAN DEPTH:</td>
<td>93 metres</td>
</tr>
<tr>
<td>RESIDENCE TIME:</td>
<td>≈ 8 years</td>
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</table>
times (Christmas and New Year holidays). Sewage effluent from septic tanks at these settlements passes into the Aniwaniwa stream or seeps directly into the lake in the vicinity of Home Bay.

Native fish and introduced species

Prior to the introduction of trout, the only native fish occurring in Lake Waikaremoana, and which are still present, were the long-finned eel (*Anguilla dieffenbachii* Gray), a bully (*Gobiomorphus cotidianus*), and a galaxid (*Galaxias brevipinnis* Günther). There may also have been other species of galaxids (P. Burstall pers.comm.), but their presence now is doubtful. Eels can no longer gain access to the lake (since hydroelectric development), but a few old and very large specimens are still present in the lake (up to at least 1.5 metres long, 14 kgs. in weight and 40 years of age).

Brown trout (*Salmo trutta* L.) were introduced to the lake in 1896 and rainbow trout (*Salmo gairdneri* Richardson) in 1907 (Burstall 1975). There are now well-established lake-migratory and stream resident (above-falls) populations of both species.

Smelt (*Retropinna lacustris* Stokell) were introduced from the Rotorua Lakes in 1948 to compensate for the anticipated adverse effects of hydroelectric development on the food resources of the trout.

The adventive aquatic weed, *Elodea canadensis*, has been
present in Lake Waikaremoana since before 1946 and is widely
distributed throughout the littoral areas of the lake.

HYDROELECTRIC DEVELOPMENT

Before 1946 the Tuai power station, which commenced power
generation in 1929, had operated only on the natural discharge
of water from the lake. In 1946 outlet modifications began,
which allowed some control over the outflow and lake level of
Lake Waikaremoana, and made feasible the siting of another
power-station (Kaitawa) between the Lake and Tuai. At first
the lake level was lowered by means of temporary siphons (aided
by an exceptionally dry summer). Twin tunnels were driven from
the Kaitawa side through the natural rock and earth-fill dam,
to connect with the intake structure, which was installed in
an excavation behind a sill close to the lake shore. When the
intake structure was completed, the sill was removed opening
the intake to the lake (Figure 2). During maximum power gen-
eration at Kaitawa the penstocks deliver water at a rate of
approximately 30 cu. metres/sec. Initially there was a loss
of trout through the intake and down the penstocks, until a
grill (4.8 cms gap) was installed across the mouth of the
intake in 1959.

Between 1948 and 1955 repeated attempts were made to seal
the subsurface leaks in the dam, but this was only partially
successful. As some of the shallower leaks were sealed, cav-
ities within the dam collapsed and an extension of the leakage
area into deeper water occurred (Figure 2). The leakage was reduced to about 5 cu. metres/sec. (approximately one third of the original flow).

The old surface overflow channel was lowered 60 cms, and in 1954 twin concrete siphons were installed beneath the surface overflow channel. These can be used to bypass Kaitawa and deliver water to the Tuai power station in the event of Kaitawa power station being closed down. They were used in December 1976 with a recorded flow of 35.4 cu. metres/sec.

Since 1946 the lake level has been maintained at a lowered level (Figure 3). This has been done to ensure stability of the natural rock and earth-fill dam, and also it provides a measure of flood protection to downstream areas.

This initial lowering of the lake level resulted in the "dewatering" of previously submerged wave-cut terraces along the papa shores and extensive areas of the old shallow littoral at stream mouth deltas. The lake level is now in the vicinity of the old "drop-off" and the littoral zone has been shifted downwards onto a steeper average slope. Assuming that there has been no significant change in water transparency, this will have resulted in a net reduction in the area of the littoral zone.

At the stream mouths deep channels have been carved through the exposed deltas. These "gauntlets" are under the influence of lake level fluctuations, having swiftly flowing water at low lake levels, and flooding back with sluggish flow
FIGURE 2. The outlet of Lake Waikaremoana before and after hydroelectric development.
at high lake levels. Because of the proximity of high water-falls close to the mouths of the majority of the streams entering the lake (Figure 1), the accessible length of streams available to spawning runs of trout is greatly restricted. These gauntlets are potentially important spawning areas particularly for rainbow trout, whose early migrant fry are not as dependent on stream nursery areas as are the brown trout fry.

LAKE LEVEL FLUCTUATIONS

The continuous record of lake level from 1931 to 1975 (Figure 3) breaks down into three reasonably distinct periods:

1. 1931 - 1946 - Before hydroelectric development - the natural fluctuations in lake level.

2. 1946 - the early 1960's - Immediately following hydroelectric development - an early period of extensive fluctuations in lake level.


Amplitude

During the recent post-hydroelectric development period the mean annual amplitude of the lake level fluctuations was 2.8 metres, which is not much greater than the natural mean annual amplitude of 2.5 metres (Figure 3), but the lake level now fluctuates about a mean lake level 4.7 metres below the natural mean lake level.
FIGURE 3. Lake level fluctuations in Lake Waikaremoana from 1931 to 1976. From data provided by the New Zealand Electricity Department.
During the early post-hydroelectric development period the mean annual amplitude of lake level fluctuations was 5.2 metres, which is more than twice the natural mean annual amplitude. During this period of time Waikaremoana was providing a much higher proportion of the hydroelectric power for the North Island than it does now. The planned hydroelectric operating range is now 607.8 - 611.4 metres a.s.l. (amplitude 3.6 metres).

Seasonal periodicity

Before hydroelectric development the lake level tended to rise in winter and fall in summer (Table II). Although the mean summer rainfall (89 cms - October to March inclusive) is not very much less than the mean winter rainfall (113 cms - April to September inclusive), increased evapotranspiration from the forested catchment during the summer months, and increased evaporation from the lake surface, will contribute to a falling lake level in summer - with an unregulated outflow.

The partial sealing of the leaks in the dam and the regulated outflow now allow the New Zealand Electricity Department to store water during the summer months for maximum power generation in the winter, (Figure 4). This has tended to reverse the natural seasonal periodicity, so that the lake level now tends to rise in summer and fall in winter (Table II).
FIGURE 4. The periodicity of lake level fluctuations in Lake Waikaremoana before and after hydroelectric development. Mean monthly rainfall at Onepoto (near the lake outlet) 1925-1974, and mean monthly power generation at the Kaitawa power station 1966-1975 - from data provided by the New Zealand Electricity Department.
Table II. The seasonal periodicity of lake level fluctuations before and after hydroelectric development.

<table>
<thead>
<tr>
<th>LAKE LEVEL</th>
<th>Before (1932 - 1941)</th>
<th>After (1966 - 1975)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RISING IN SUMMER</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>FALLING IN WINTER</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>FALLING IN SUMMER</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>RISING IN WINTER</td>
<td>7</td>
<td>2</td>
</tr>
</tbody>
</table>

SEASONAL TIMING OF EXTREME LOW LAKE LEVELS

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>LATE SUMMER - EARLY WINTER</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>MID WINTER</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>LATE WINTER - EARLY SUMMER</td>
<td>0</td>
<td>9</td>
</tr>
</tbody>
</table>
The major cycle

Before 1946 the lake level tended to fluctuate on an annual cycle about a reasonably steady mean annual lake level. Immediately following hydroelectric development, although an annual cycle is still present, a "major cycle" spanning 2-4 years is superimposed, and this is still present, but less marked, in the recent post-hydroelectric development period (Figure 4).

The major cycle is a consequence of hydroelectric utilization of the lake. The more or less constant (or increasing) annual demand for power accentuates the effects of dry years between successions of wet years. Dry winters (e.g. 1964, 1969 - Figure 5) predispose to extreme drawdown, and a succession of wetter than average years (e.g. 1970, 1971 - Figure 5) produce a "long term" upward trend in the lake level.

Rate of rise and fall

With the intake closed, the rate of rise in lake level for any given inflow will have increased since hydroelectric development due to the partial sealing of the leaks, and the total absence, since 1946, of a surface overflow.

The rate of drawdown during maximum power generation at Kaitawa is, of course, partly dependent on the inflows, but averages about 3 cms/day, and may increase to about 6 cms/day at low lake levels and low inflows.
FIGURE 5. Lake level fluctuations in Lake Waikaremoana and six monthly rainfall (Onepoto) and power generation (Kaitawa) 1961 - 1976. The six monthly periods are October to March inclusive (summer) and April to September inclusive (winter).
During maximum power generation at Kaitawa the outflow from the lake, 30 cubic metres/sec., is more than twice the natural outflow, when there was no surface overflow, ≈ 14 cubic metres/sec. (Anderson 1948).

MATERIALS AND METHODS

PHYSICAL

Surveys of the lake shore

Aerial photographs of the lake taken before and after hydroelectric development (N.Z. Aerial Mapping) were used to determine the positions of the pre-1946 and the 1971 shorelines of the lake, 615.7 metres a.s.l. and 610.5 metres a.s.l. respectively (an elevation difference of 5.2 metres) — and thus define the shallow areas of the pre-1946 lake-bed, which were "dewatered" as a result of lowering the lake level with hydroelectric development in 1946. Henceforth this dewatered area of the old lake bed will be referred to as the "lost littoral". Its lower boundary is delineated on sheltered areas of the lake shore by the lower limits of terrestrial vegetation (which are not entirely stable), but it does not include the shallow areas of the present littoral zone, which are intermittently exposed by hydroelectric drawdown.

Work sheets showing the lost littoral were prepared from the aerial photographs (scale 1:12,667), and, along
with the relevant sections of the 1971 aerial photograph, were used during an aerial survey of the entire shoreline by RNZAF Iroquois helicopter in September 1976. Doubtful areas of the lost littoral on the aerial photograph (e.g. areas in shadow or covered by scrub) were checked for accuracy on the work sheets, and the nature of the vegetation cover of the lost littoral was recorded.

Two separate shoreline surveys have been carried out by boat. The first, during October to December 1974, was a detailed survey of the present littoral zone to record shoreline geology, development of wave cut platforms, substrate in the shallow littoral zone, and distribution of aquatic macrophytes. The second survey in October 1976 was carried out to record the geology of the pre-1946 shoreline (Figure 6).

Planimetry

The bathymetry of Lake Waikaremoana with isobaths at 20 metre depth intervals was completed by Mr. J. Irwin of the New Zealand Oceanographic Institute in September 1972 (Irwin 1977). This chart (scale 1:15,840) was used to measure the areas enclosed by the shoreline and isobaths with a polar planimeter, the mean of three readings being taken.

A second chart was prepared from the 1971 aerial photograph and work sheets (scale 1:12,667). This was used
to measure the area of the lost littoral and length of shoreline before and after hydroelectric development.

The areas of the lost littoral and present 0-20 metre depth zone, and the length of shoreline were measured in sections in relation to shoreline geology.

The area of the present littoral zone was estimated by using a correction factor of 17/20 on the measurements of the present area of the 0-20 metre depth zone. The area of the pre-1946 littoral zone was estimated by adding the area of the lost littoral to (the area of the present 0-20 metre depth zone \( \times \frac{17 - 5.2}{20} \)).

Lake volume, mean depth, shoreline development and the area of the limnetic zone before and after hydroelectric development were also calculated from the above measurements.

Water transparency and temperature

Temperature profiles in the lake and water transparency were recorded at least monthly between October 1974 and July 1977 at two stations - one at the centre of the main lake, and the other in the Wairaumoana arm (Figure 1). Temperature profiles were recorded at metre intervals down to 55 metres depth with a Y.S.I. temperature/oxygen meter, model 51A. Water transparency was measured with a 20 cm. diameter Secchi disc.
Lake level, power generation and rainfall

The charts of lake level fluctuations were prepared from daily records of the lake level kept by the New Zealand Electricity Department. A staff gauge was installed near the laboratory at Home Bay for recording lake level on sampling days. Data on rainfall at Onepoto (close to the lake outlet) and power generation at the Kaitawa power station were provided by the New Zealand Electricity Department.

LITTORAL BENTHOS

Ekman dredge sampling

Trial Ekman dredge sampling was carried out at scattered localities around the lake shore in conjunction with the shoreline survey. The substrate below the drawdown zone was found to be more or less uniform throughout the littoral areas of the lake, consisting of fine papa silt, which was ideal for Ekman sampling. The substrate in the drawdown zone was much more variable, and in many instances (e.g. stones, boulders or bedrock of sandstone and papa) it was impossible to sample with an Ekman dredge. In some sheltered bays the substrate in the drawdown zone also consisted of fine papa silt, and such was the case at Hautaruke Bay which was chosen as the main sampling station (Figure 6).

The transect at Hautaruke Bay was clear of standing or fallen tree stumps, and the shallow littoral area contained a relatively low growth of macrophytes, such that the macrophytes
and their underlying substrate and roots were obtained in each Ekman sample. Scuba surveys were carried out along the sampling transect on three occasions, and during one of these the slope of the littoral and lower limits of the "mixed" and Nitella zones were plotted (Figure 7).

A second station close to Home Bay was sampled regularly in conjunction with the Hautaruke Bay sampling programme to examine the possible effects of sewage enrichment, but the results from this second station are not presented here.

The littoral invertebrate fauna was sampled over a 12 month period (April 1975 - April 1976) at Hautaruke Bay. Sampling was carried out on a monthly basis when possible (July, October and December 1975 samplings were missed due to other commitments).

On each sampling occasion single Ekman dredge (15 cm X 15 cm) samples were taken at metre depth intervals from 1 down to 9 metres, and at alternate metres between 9 and 20 metres, along the transect through the littoral zone (Figure 7). The depth intervals sampled were in relation to a theoretical "zero" lake level (609.6 metres a.s.l.), which was the lower limit of terrestrial vegetation during the sampling period. Samples were washed and sieved through a 0.8 mm bronze wire mesh and sorted live the day they were obtained.

In addition to the monthly sampling, 10 replicates were taken at each of the three depths (2, 5 and 12 metres), on separate occasions, to examine sampling variability in the
FIGURE 6. Lake Waikaremoana showing shoreline geology, lost littoral (black), Bathymetry (20,100 & 200 metre isobaths from the bathymetry of Lake Waikaremoana, Irwin 1972), and station locations.
FIGURE 7. Diagrammatic transects of 
a) the littoral zone at Hautaruke Bay - benthos sampling station and,  
b) the netting stations showing the positioning of the gillnets.
drawdown, mixed and Nitella zones respectively.

Statistical procedure

A one-way non-parametric analysis of variance (The Kruskal-Wallis Test) was used to test for significant differences at p<0.05 in the depth distribution of animals between seasons. Each sample collected during the monthly samplings within each season was used as a replicate of the respective depth zone.

ZOOPLANKTON AND LARVAL FISH

Zooplankton samples were taken monthly between October 1975 and August 1977 at two stations - the Te Puna and Red Reef offshore netting sites (Figure 6). Two vertical hauls from 55 metres depth to the surface were taken at each sampling site on each sampling occasion using a 25 cm diameter Wisconsin nylon net (10 meshes/mm).

Two replicate samples of the larval fish were obtained at the same stations on the same occasions between August 1976 and August 1977. A heavy-rimmed 55 cm diameter net (5.3 meshes/mm) was used, which sampled vertically from the surface down to a depth of 75 metres. At this point the handline was allowed to tighten, snaring the net, and tilting the heavy rim through 90°, and then immediately commencing the retrieve of the closed net to the surface (Figure 8).

Echosounder runs of approximately 400 metres were made at the offshore netting stations in conjunction with the sampling
FIGURE 8. The net used for sampling larval fish.
of the larval fish using a Furuno FG 11 Mark 3 echosounder (50 khz) at a setting of gain 4. Larval bullies (*Gobiomorphus cotidianus*) are in a similar size range to *Chaoborus* larvae and with their gas-filled swim-bladders produce deep scattering layers on the echosounder tracings similar to those described for *Chaoborus* larvae (Northcote 1964). Larval smelt (*Retropinna lacustris* Stokell) do not have a gas-filled swim-bladder, and were found to produce no scattering layer on the echosounder on those sampling occasions when they were plentiful, but larval bullies were absent.

*Daphnia* in the August 1976 to June 1977 Wisconsin samples were counted in entirety and together with the remaining Wisconsin samples have been examined and counted by Dr. M.A. Chapman of Waikato University.

The larval fish samples were counted in entirety and total length measurements were made on each larval fish using a precision caliper fitted with needle-point extensions to the measuring arms.

**TROUT**

Netting programme

Samples of trout were obtained by gillnetting at intervals of two months from October 1975 to December 1976. Two stations were used - one in the main lake, Red Reef, and the other in Waïraumoana, Te Puna (Figure 6). At each station separate nets were set in the limnetic zone, in the deep littoral zone, and
in the drawdown zone (Figure 7).

The offshore net (in the limnetic zone) was set at the surface in water 80-100 metres deep. This net was 60 metres long and 10 metres deep.

An onshore net was set at the surface over the deep littoral in water 10-15 metres deep; this net was 60 metres long and 5 metres deep. Both this onshore net and the offshore net contained six 10 metre long panels of different mesh sizes: 2.5, 3.8, 5.1, 7.0, 7.6 and 10.2 cms - monofilament nylon netting.

In addition two small nets - 15 metres long and 2.5 metres deep were used in the drawdown zone, one with a mesh size of 2.5 cms, the other with a mesh size of 5.1 cms. These small nets in the drawdown zone were not used during the first two nettings - i.e. October 1975 and December 1975.

The nets were set before dusk and lifted after dawn the next day. The distribution of trout within and between the nets was recorded; species, sex, length, weight, and state of the gonads were recorded. The entire stomach was removed and preserved in 10% formalin for later examination, together with a sample of scales.

The distinction between immature fish and "previous spawners" could be made in most instances by macroscopic examination of the gonads, but where there was any doubt scales were examined later for spawning marks, which were well developed in both rainbow and brown trout.
Stomach analysis

The stomach was divided at the pyloric flexure, and only the anterior portion was used for detailed analysis of the contents. The smaller food items were examined and sorted at X 20 - 40 magnification under a dissecting microscope. The volume of the different food items was measured to the nearest 0.1 ml by displacement of water in a graduated glass cylinder. The volume of the pyloric contents was also measured to give the total volume of the stomach contents.
RESULTS

PHYSICAL

Morphometric Changes

The initial lowering of the lake level with hydroelectric development reduced the surface area of the lake from 54.8 to 51.4 km$^2$ (Table III). 3.4 km$^2$ of the pre-1946 shallow littoral area was lost. The estimated gain in littoral area due to the pre-1946 sublittoral, which is now included in the euphotic zone and has become the lower extremity of the new littoral, was approximately 2.1 km$^2$ – and this was the extent of the reduction in the limnetic area.

There has therefore been a disproportionate percentage reduction in the littoral area ($\approx$ 17% net reduction) as compared with the limnetic area ($\approx$ 4% reduction) and this has altered the ratio of littoral to limnetic areas from 1 : 5.8 to 1 : 6.7.

Almost half of the net reduction in the littoral area was a result of the loss of previously submerged stream-mouth deltas, and to a slightly lesser extent the loss of wave-cut terraces on the exposed papa shores (Figure 6). There has been little net reduction in littoral area along mixed shores, and no net reduction along the sandstone shores.

The slight reduction in shoreline development is due in part to the loss of islands, which now form peninsulas.

There has been little change in the mean depth of the
Table III. Morphometric changes in Lake Waikaremoana following hydroelectric development of the lake.

<table>
<thead>
<tr>
<th></th>
<th>PRE-HYDROELECTRIC DEVELOPMENT</th>
<th>POST-HYDROELECTRIC DEVELOPMENT</th>
<th>LOSS</th>
</tr>
</thead>
<tbody>
<tr>
<td>SURFACE AREA</td>
<td>km²</td>
<td>54.8</td>
<td>51.4</td>
</tr>
<tr>
<td>LENGTH OF SHORELINE</td>
<td>km</td>
<td>103.5</td>
<td>93.2</td>
</tr>
<tr>
<td>(INCLUDING ISLANDS)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SHORELINE DEVELOPMENT</td>
<td></td>
<td>3.95</td>
<td>3.67</td>
</tr>
<tr>
<td>MEAN DEPTH</td>
<td>metres</td>
<td>91.7</td>
<td>92.7</td>
</tr>
<tr>
<td>ESTIMATED AREA OF LITTORAL ZONE</td>
<td>km²</td>
<td>8.1</td>
<td>6.7</td>
</tr>
<tr>
<td>(&gt; 17 METRES DEPTH)</td>
<td></td>
<td>46.7</td>
<td>44.6</td>
</tr>
<tr>
<td>RATIO OF AREAS OF LITTORAL:LIMNETIC</td>
<td>1 : 5.8</td>
<td>1 : 6.7</td>
<td></td>
</tr>
</tbody>
</table>
lake (in fact a slight increase), and therefore no significant change in the ratio of the volumes of epilimnion to hypolimnion. The 5% reduction in the lake volume will have had an insignificant effect on the residence time of approximately 8 years.

Thermal conditions & water transparency

Thermal stratification lasts for about 6 months of the year, December to May (Figure 9). Climatic variation between the years 1974 - 1977 produced appreciable differences between years in the depth and strength of thermal stratification and maximum surface temperatures (Figure 9). The considerable depth of the thermocline reflects the generally windy conditions of the Waikaremoana climate.

The thermocline, apart from the first 1-2 months of the period of thermal stratification, lies below the lower limit of the littoral zone, and so throughout most of the year the entire littoral zone is exposed to more or less the same seasonal changes in water temperature.

Secchi disc readings varied from 5.5 to 17.5 metres with a mean of 11.5 metres. There is a significant negative correlation (p<0.01) between water transparency (Secchi disc readings) and lake level, (Spearman's rank correlation coefficient, r = -0.61). The greatest reduction in water transparency occurred immediately after an exceptional flood during the New Year period 1975/76, when heavy sediment loads and much
floating woody debris entered the lake.

The amplitude of lake level fluctuations during the study period (October 1974 - July 1977) was 3.54 metres; 1.60 metres "damming up" above the theoretical zero lake level (609.6 metres a.s.l.) and 1.94 metres drawdown below. During each of the 3 years 1975, 1976 and 1977, "damming up" with flooding of terrestrial vegetation and soil occurred during late summer or early winter, lasting for 2-5 months. Extreme drawdown occurred during late winter (August) 1976.

Dissolved oxygen

Only one reliable dissolved oxygen profile was obtained. This was towards the end of the period of thermal stratification in late April 1975 (Figure 10). Dissolved oxygen in the hypolimnion down to 55 metres depth was close to full saturation for the temperatures observed and the altitude (Hutchinson 1957), but a metalimnial oxygen minimum was present. Echo-sounder runs during summer showed that the larval bullies concentrate at the thermocline during the daylight hours.

AQUATIC MACROPHYTES

Rooted aquatic macrophytes extended down to a depth of 17.5 metres at Hautaruke Bay (Figure 7). This was taken to be the lower limit of the littoral zone and commencement of the sublittoral (Macan 1951). During trial Ekman sampling and scuba surveys at several other locations in the main lake,
the lower limit of rooted macrophytes was also found to occur at about 17-18 metres depth, with the exception of the littoral areas in the proximity of the motor camp at Home Bay, where the lower limit occurred at 15-16 metres depth.

Extreme drawdown during the late winter of 1973 (Figure 3) extended ~ 3 metres below the theoretical zero lake level. In sheltered littoral areas of the lake the upper boundary of continuous macrophyte beds provided a very clear demarcation of the lower limit of this drawdown, which had been the lowest lake level since the winter of 1969. On shores exposed to much wave action rooted macrophytes were sparse or absent in littoral areas less than ~ 5 metres depth.

In the lower "drawdown zone" sparse clumps of some native aquatic macrophytes had survived in most sheltered areas of the lake, but the adventive weed, _Elodea canadensis_, was not found in the drawdown zone during the spring of 1974. During the higher lake levels of 1975 and early 1976 _Elodea_ invaded the lower drawdown zone by means of lateral vegetative shoots.

At Hautaruke Bay extending from the lower limit of drawdown (3 metres depth) down to 8 metres depth there was a "mixed zone" of _Nitella sp._, _Myriophyllum sp._ and _Potamogeton sp._ with a sparse intermingled growth of _Elodea canadensis_. This mixed zone was typical of most other areas of the lake examined, except in the vicinity of Home Bay, where the mixed zone was replaced by a dense monoculture of _Elodea canadensis_.
From 8 metres depth down to 17.5 metres depth there was a monoculture of Nitella sp. forming the "Nitella zone". During the early summer of 1975/76 there was a gradual extension of Nitella into deeper water, but following the sudden rise in lake level in January 1976, and reduced water transparency, there was a die-off of the deeper Nitella beds, which was apparent from examination of the macrophytes obtained in the Ekman samples.

During the summer of 1974/75 the emergent species of aquatic macrophytes (Myriophyllum sp. and Potamogeton sp.), in the shallow littoral zone of sheltered areas of the lake, penetrated the lake surface and successfully flowered, but during the summers of 1975/76 and 1976/77 the rising and maintained lake levels during summer prevented successful flowering of these species.

LITTORAL BENTHOS

Sampling variability

The variance to mean ratio, which is an index of dispersion, is greater than one for total animals, total molluscs, total insects and oligochaetes at each of the three depth intervals sampled (Table IV). This suggests contagious distributions, which are usual for most benthic invertebrates (Elliott 1971). However, only at the 11-12 metre depth interval for the total molluscs is this a significant departure from unity (at p<0.05 $\chi^2$ Table) indicating that the remainder
Table IV. Sampling variability within the drawdown (at 2-3 m, 27th May '76), mixed (at 5-6 m, 9th June '76), and Nitella (at 11-12 m, 29th March '76) zones at Hautaruke Bay.

\[ n = 10 \text{ replicates at each depth interval.} \]

<table>
<thead>
<tr>
<th>Depth Interval (metres)</th>
<th>Mean Number</th>
<th>95% Confidence Limits</th>
<th>Variance</th>
<th>Variance Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOTAL ANIMALS</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 - 3</td>
<td>221</td>
<td>± 24</td>
<td>1532</td>
<td>6.9</td>
</tr>
<tr>
<td>5 - 6</td>
<td>405</td>
<td>± 39</td>
<td>3955</td>
<td>9.8</td>
</tr>
<tr>
<td>11 - 12</td>
<td>463</td>
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<td>12.7</td>
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<tr>
<td>TOTAL MOLLUSCS</td>
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<tr>
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<td>± 12</td>
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<td>± 9</td>
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<tr>
<td>11 - 12</td>
<td>266</td>
<td>± 47</td>
<td>5660</td>
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<td>TOTAL INSECTS</td>
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<td>± 32</td>
<td>2666</td>
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<tr>
<td>11 - 12</td>
<td>130</td>
<td>± 17</td>
<td>711</td>
<td>5.5</td>
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<td>OLIGOCHAETES</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 - 3</td>
<td>68</td>
<td>± 18</td>
<td>840</td>
<td>12.4</td>
</tr>
<tr>
<td>5 - 6</td>
<td>32</td>
<td>± 11</td>
<td>333</td>
<td>10.4</td>
</tr>
<tr>
<td>11 - 12</td>
<td>66</td>
<td>± 11</td>
<td>336</td>
<td>5.1</td>
</tr>
</tbody>
</table>

\[ * = \text{significant departure from unity (p<0.05 Table of } \chi^2) \]
could be randomly distributed.

Some of the problems associated with sampling of benthic invertebrates in lakes, and causes of sampling variability are described by Northcote (1952). Among those relevant to this study are contagious distributions in relation to quadrat size, operation of the sampling equipment, heterogeneity of substrate, and variability due to changes in depth and season. Northcote found the greatest variability in the shallow littoral (0 - 5 m.), and attributed this to the wide variation in substrate within this depth zone.

The scale of contagious distributions in relation to the area enclosed by the sampler is an unavoidable problem, because it varies considerably between different taxa of benthic invertebrates, and so the choice of quadrat size is unlikely to be appropriate for all taxa (Elliott 1971). It appears that at Hautaruke Bay in the upper Nitella zone this was a problem with total molluscs.

At Hautaruke Bay heterogeneity within zones in the sampling area was minimal. The inorganic substrate was uniform throughout the littoral zone. There was little gross clumping of the different macrophyte species in the mixed and drawdown zones, and the density of macrophyte growth was relatively homogeneous within zones, the greatest variability in density occurring with depth in the Nitella zone. Although throughout the lake the shallow littoral areas showed the greatest heterogeneity within the littoral zone, within the sampling area this
was not so.

The papa silt substrate was ideal for Ekman sampling and free from coarse debris, which might interfere with closing of the jaws. The choice of a 0.8 mm mesh was perhaps not ideal for chironomids and oligochaetes. Many of their early instars and small individuals would have been lost during washing and sieving of the samples.

Pooling of the data over the twelve month period introduces seasonal changes as a cause of variability, and pooling the data from different depths within zones introduces depth as an additional cause of variability. The 95% confidence limits on the means of 10 replicates taken on the same day and from the same depth give an indication of less variability than could be expected in the results of the sampling programme.
Depth distribution

The mean number of total animals for the twelve month sampling period in the upperdrawdown zone is less than 1000/m² (Figure 11) with an order of magnitude increase in numbers in the lower drawdown zone (≈ 9000/m²). There is little change in mean numbers of total animals throughout the lower drawdown, mixed, and upper Nitella zones (1 - 10 metres), but there is a decrease in numbers throughout the lower Nitella zone to the sublittoral. Molluscs, insects, and oligochaetes account for > 95% of the numbers of the macro-invertebrate fauna (Figure 12). It is the molluscs and insects which contribute most to produce the overall pattern of depth distribution. Oligochaetes show a maximum density at 1 - 3 metres depth, which, in the profile of total animals, masks the slightly reduced numbers of insects and molluscs in the lower drawdown zone (Figure 11).
FIGURE 11. The depth distribution of total animals, molluscs, insects, and oligochaetes in the littoral zone at Hautaruke Bay. The mean number of individuals per Ekman sample from each metre depth interval during the 12 month sampling period, expressed as number of animals per square metre. \( \text{(n)} \) = sample sizes.
Composition

Several taxa, which are prominent in the fauna of Northern Hemisphere temperate lakes are absent (e.g. Chaoborinae) or rare (e.g. Ephemeroptera, Plecoptera, Isopoda, Amphipoda) in New Zealand Lakes (Marples 1962, Forsyth 1975).

Lake dwelling Plecoptera are absent in Lake Waikaremoana, as are truly lake-dwelling Ephemeroptera. However, during the winter months nymphs of one of the stream-dwelling mayflies (Zephlebia sp.) do colonize the stony shores of the lake in the proximity of stream mouths, but disappear after emergence in late spring/early summer. Amphipods, although present within the catchment of Lake Waikaremoana, are rare in the inflowing streams, and were not found in the lake. In New Zealand semi-terrestrial species of Amphipoda are common in the damp leaf litter of forest floors (Dr. M.A. Chapman pers. comm.) and the two specimens found in the inflowing streams may have originated from this source.

The Odonata and Trichoptera are therefore of much greater importance in New Zealand lakes - particularly with respect to trout food.
FIGURE 12. The composition of the littoral invertebrate fauna at Hautaruke Bay, Lake Walkaremoana, showing the mean number of individuals per square metre for each metre depth interval of the littoral zone during the 12 month sampling period.
Even those groups of animals, which are present in New Zealand lakes, show a rather low species diversity. Among the littoral species of chironomids in Lake Waikaremoana there are at least 6 species, but probably no more than 10 (Forsyth 1975) - compared with some Scandinavian lakes e.g. Lake Ankarvattnet, Sweden: 56 species of littoral chironomids, and the regulated lake Blasjön: 27 species (Grimas 1961), and a storage reservoir in England: 57 species of chironomids (Mundie 1957).

The greatest diversity in the littoral invertebrate fauna of Lake Waikaremoana occurred in the shallow littoral. Nymphula nitens, ostracods, chydorids, planarians, ceratopogonids and at least 2 species of chironomids were only found at depths less than 7 metres (Figure 12).

The sphaeriids and two species of Trichoptera, Pycnocentrodes sp. and Paroxyethira hendersoni, occur throughout the littoral, but show maxima in the drawdown and/or sublittoral zones.

The other 2 species of Trichoptera, the Odonata, total chironomids and the two abundant species of gastropods, Potamopyrgus sp. and Gyraulus sp., all more or less show a similar depth distribution to the profile of total animals.

Two of the less common gastropods, Phyastra sp. and Simlimnaea sp., occur within more localized depth zones. Phyastra sp., which was more abundant during summer, occurred
largely in the Nitella zone, and *Simlimnaea sp.* showed a maximum density in the mixed and lower drawdown zones and was more abundant during winter.

Only a single koura (*Paraneophrops planifrons* - the freshwater crayfish) was taken in the Ekman samples; they are probably able to take evasive action. They were not infrequently seen during scuba surveys.

Seasonal Changes in depth distribution

Total animals

The three series of samples taken during May to August inclusive were combined to examine the profile of winter depth distribution, and the three series of samples taken during November to February inclusive were combined to give the summer profile.

For statistical comparison between summer and winter depth distribution the littoral zone was divided into the upper and lower drawdown zone, the mixed zone, and the upper and lower Nitella zone (Figure 13). Sample sizes were too small within the upper drawdown and sublittoral zones to make valid statistical comparisons between winter and summer in these depth intervals.

There is little difference in the mean number of total animals within the entire littoral zone between winter and summer (6200/m² in winter, 6700/m²† in summer), but there are

† mean of means from each 2 metre depth interval of the littoral zone.
FIGURE 13. Seasonal changes in the depth distribution of total animals at Hautaruke Bay.

(n) = sample sizes in each 2 metre depth interval.

* = significant difference at p<0.05 Kruskal-Wallis Test between summer and winter in the depth zones indicated by the vertical bars.
significant differences between winter and summer in the depth distribution. During winter the maximum density of animals occurs in the lower drawdown and mixed zones with significantly greater numbers than occurred in the mixed zone during summer (p<0.05 Kruskal Wallis Test). During summer there is a more even distribution of animals throughout the littoral zone, with a bulge in numbers in the Nitella zone. The increased numbers of animals in the Nitella zone during summer is only significantly greater than winter (at p<0.05 Kruskal Wallis Test) within the lower Nitella zone.

Total molluscs, total insects and oligochaetes

There may be some overall increase in the numbers of total molluscs within the entire littoral zone during summer from a mean of 2850/m² in winter to 3250/m² in summer, but there appears to be little difference between summer and winter in the numbers of insects and oligochaetes (Figure 14). However, these seasonal comparisons in overall numbers, where there are seasonal changes in depth distribution, are not strictly valid, because of the uneven slope and configuration of the littoral (Figures 6 & 7).

Both total molluscs and total insects show maximum densities in the mixed zone during winter, with a downward shift during summer. This downward shift is deeper in molluscs, which show greater numbers during summer than winter throughout
FIGURE 14. Seasonal changes in the depth distribution of molluscs, insects and oligochaetes at Hautaruke Bay. Asterisk indicates a significant difference (at $p < 0.05$, Kruskal-Wallis Test) between summer and winter in the depth zones indicated by the vertical bars. ($n$) = sample sizes.
the Nitella zone, whereas insects show an increase in numbers in the upper, but not the lower, Nitella zone during summer.

There is an increase in numbers of oligochaetes in the lower drawdown zone during summer, but there is no statistically significant difference between summer and winter in the depth distribution (at \( p < 0.05 \) Kruskal Wallis Test).

Seasonal changes - Molluscs

The gastropods, *Potamopyrgus antipodarum* and *Gyraulus sp.*, both show the same seasonal patterns of increased numbers in the Nitella zone during summer, and increased numbers in the mixed zone during winter (Figure 15). These differences between summer and winter are statistically significant (\( p < 0.05 \) Kruskal Wallis Test) in the lower Nitella zone and in the mixed zone, and for *Gyraulus sp.* in the lower drawdown zone also.

The bivalves show a different seasonal pattern. They have a more or less even distribution throughout the littoral zone during winter, but during summer they show an increase in numbers in the lower drawdown and sublittoral zones, and a decrease in the mixed and Nitella zones. These seasonal differences are not statistically significant.

Seasonal changes - Odonata and Lepidoptera

The two species of Odonata - the dragonfly *Procordulia grayi* and the damselfly *Xanthocnemis zealandica* - show little
FIGURE 15. Seasonal changes in the depth distribution of gastropods and bivalves at Hautaruke Bay. Asterisk indicates a significant difference (at p < 0.05, Kruskal-Wallis Test) between summer and winter in the depth zones indicated by the vertical bars.
difference in total numbers between summer and winter. The size frequency distributions of the larvae following the period of emergence of the adults in summer suggests that many of the larvae of these two species take more than one year to reach the final instar, and hence there is not such a great decline in numbers following emergence of the adults in summer. This is not unusual in Odonata (Macan 1977, Pendergast & Cowley 1966).

Both species shown an upward shift in the maximum densities of larvae during the winter months (Figure 16). The maximum density of *P. grayi* during winter occurs in the lower drawdown zone, whereas the maximum density of *X. zealandica* during winter occurs deeper than *P. grayi* - in the mixed zone.

The adult male dragonflies, *P. grayi*, take up station close to the water's edge, and exhibit territorial behaviour, clashing with intruding males and seizing any passing female. Ovipositing by *P. grayi* occurs during November to January. The adult females deposit single eggs at the surface of the water over the littoral zone, which sink to the bottom and take 1-2 months to hatch (Armstrong 1958). Early instar larvae were found widely dispersed throughout the littoral zone below 2 metres depth by late summer (February).

The adult damselflies, *X. zealandica*, deposit their eggs on the stems or leaves of emergent macrophytes (Pendergast & Cowley 1966). The early instar larvae were found down to 19 metres depth by late summer (January), but the greatest
FIGURE 16. Seasonal changes in the depth distribution of Odonata and Lepidoptera at Hautaruke Bay. Asterisk indicates a significant difference (at p < 0.05, Kruskal-Wallis Test) between summer and winter in the depth zones indicated by the vertical bars.
numbers occurred between 5 and 10 metres depth.

The aquatic larvae of the small moth, *Nymphula nitens*, take a single year to complete their life cycle. They are confined to the shallow littoral, and their numbers are temporarily reduced following emergence of the adults in summer (Figure 16).

**Seasonal changes - Trichoptera**

The large caddis, *Triplectides* sp., which takes a single year to complete its life cycle, shows a decrease in numbers in all zones during the summer months following emergence of the adults (Figure 17). Pupae were found attached to aquatic macrophytes during December, January and February at depths ranging from 1 to 14 metres, with a maximum at 5 metres depth.

The small sandgrain-cased caddis, *Pycnocentrodes* sp., shows no statistically significant difference in numbers or depth distribution between summer and winter, although the greatest numbers were found in the drawdown and lower Nitella zones with a paucity, particularly during summer, in the mid-littoral. Pupae were not found during Ekman sampling.

The finding of the pupae (attached to aquatic macrophytes) throughout the year suggests that the small hydroptilids, *Paroxyethira tillyardi* and *Paroxyethira hendersoni*, pass through at least 2 generations in a year. The winter generation of *P. tillyardi* is concentrated mainly in the mixed and lower drawdown zones with a maximum number of pupae found in
FIGURE 17. Seasonal changes in the depth distribution of Trichoptera at Hautaruke Bay. Asterisk indicates a significant difference (at $p < 0.05$, Kruskal-Wallis Test) between summer and winter in the depth zones indicated by the vertical bars.
October at 4 - 6 metres depth. The summer generation is concentrated mainly in the Nitella zone with maximum numbers of pupae occurring in January between 9 to 15 metres depth.

There is no statistically significant difference in the numbers or depth distribution of *P. hendersoni* between summer and winter, although the greatest numbers were found in the drawdown zone in winter, and in the sublittoral in summer, with a paucity of numbers in the mid-littoral. Pupae were found at depths ranging from 1 to 20 metres.

Seasonal changes - chironomids

There is a slight downward shift in the depth distribution of Chironominae in summer compared with winter, but the only statistically significant difference is a greater number in the lower Nitella zone during winter (Figure 18).

The Tanypodinae show no significant difference in numbers or depth distribution between summer and winter.

The unidentified group of chironomids include at least 4 species with representatives of the Orthocladiinae. There is an overall decrease in numbers during summer, but this is not statistically significant.

TROUT

Composition of the total catch

The size, maturity and species composition of the total catch of trout in the gillnets during the period February 1976
Figure 18. Seasonal changes in the depth distribution of chironomids at Hautarupe Bay. Asterisk indicates a significant difference (at p < 0.05, Kruskal-Wallis Test) between summer and winter in the depth zones indicated by the vertical bars.
to December 1976 inclusive (Figure 19) shows that 82% of the
total catch were rainbow trout; 18% were brown trout. 80% of
the rainbow trout were immature whereas only 53% of the brown
tROUT were immature. The mature brown trout have a signifi-
cantly greater mean length (56.5 cms, 95% C.L. ± 1.4) than
the mature rainbow trout (mean length 51.8 cms, 95% C.L. ±
0.9).

Spatial distribution

The length frequency distributions of trout caught in the
drawdown, deep littoral and limnetic nets are shown in Figure
20. Considering first the rainbow trout: - in the drawdown
zone the catch consisted of small juveniles (< 26 cms.) and
large, mostly mature, fish, with only a small proportion of
intermediate-sized fish. In the limnetic zone the catch con-
sisted largely of intermediate-sized juveniles. Over the
deep littoral zone the catch shows a bimodal length-frequency
distribution of intermediate-sized juveniles, very few small
juveniles (< 26 cms), and a group of larger, mostly mature
fish. There is no significant difference in size between the
mature rainbow trout caught in the deep littoral and in the
drawdown zones.

The distribution of brown trout in the limnetic, deep
littoral, and drawdown nets shows a similar, but less clearly
defined, pattern according to size and maturity (N.B. smaller
sample sizes), but in addition there is a significant difference
FIGURE 19. The composition of the total catch of trout in the gillnets (February 1976 - December 1976) from both stations, according to species, size and maturity. (n) = sample sizes.
FIGURE 20. The percentage length composition in 2 cm. groupings of trout caught in gillnets in the drawdown zone, in the deep littoral zone and in the limnetic zone, from both stations (February 1976 - December 1976 inclusive). Immature fish (black); mature fish (cross-hatched). (n) = sample sizes.
in size between the mature brown trout caught in the deep littoral and in the drawdown zones. The mean length of mature brown trout caught in the drawdown zone, 57.5 cms, is significantly greater than the mean length of mature brown trout caught in the deep littoral zone, 55.1 cms (p<0.01 Kruskal Wallis Test).

Stomach analysis

The food items recorded during stomach analysis were categorized as:

1. Limnetic food, which consisted of *Daphnia carinata*, larval smelt, larval bullies (and an insignificant quantity by volume of chironomid pupae), all of which are small (<3 cms in length).

2. Littoral food, which consisted of littoral invertebrates ranging in size up to dragonfly larvae of ≈ 2.5 cms, and koura (the freshwater crayfish, *Paranephrops planifrons*) up to ≈ 12 cms length, subadult and adult bullies up to ≈ 10 cms length, and in the case of rainbow trout, the shoots of aquatic macrophytes, which may only have been taken incidentally along with an invertebrate prey item.

3. Subadult and adult smelt, treated as a separate category, because, although they were observed in schools in the littoral areas from October to April, Jolly (1967) found that in Lakes Taupo and Rotorua they remain partially pelagic in behaviour and feeding.
4. Terrestrial insects - largely Coleoptera and cicadas.
5. Frogs - *Hyla aurea*.
6. Debris - other than aquatic macrophytes.

The smaller juvenile rainbow trout contained largely limnetic food in their stomachs (Figure 21), and *Daphnia* were an important food item particularly during spring and early summer. *Daphnia* were found in the stomachs of immature rainbow trout of up to 54 cms. length, but *Daphnia* were not found in the stomachs of any brown trout.

Terrestrial insects formed a significant component of the diet of rainbow trout during summer (November to February inclusive), and, overall, formed 10 - 20% of their diet, but they contributed insignificantly to the diet of brown trout.

Rainbow trout contained an increasing amount of debris in their stomachs with increasing age and size, but debris formed a negligible proportion of the stomach contents of brown trout.

Subadult and adult smelt were an important food item for both rainbow and brown trout. They formed an increasing proportion of the diet of rainbow trout with increasing age and size, but they formed an even greater proportion of the diet of brown trout; 50 - 70% in the immature brown trout, and 30 - 40% in the previous spawner brown trout, in which bullies became the most important food item. Brown trout were more piscivorous than rainbow trout.
Frogs were only found in the stomachs of large brown trout (> 55 cms length) between November and January inclusive.

The only littoral invertebrate, which contributed significantly by volume or occurrence to the diet of brown trout, was the late instar larvae of the dragonfly, _Procordulia grayi_. Rainbow trout contained a greater variety of littoral invertebrates; they also fed upon the late instar larvae of _P. grayi_, but took early instar larvae as well. _Triplectides_ larvae were an important item in the diet of larger rainbow trout, but were not found in any brown trout stomachs. Damselfly larvae, _Xanthochnemis zealandica_, formed a significant proportion by occurrence, but not volume, in the diet of rainbow trout.

There was an increasing percentage of littoral food, and a decreasing percentage of limnetic food, in the diet with increasing age and size in both brown trout and rainbow trout.

The limnetic food resources

Seasonal changes in the abundance of _Daphnia carinata_, larval smelt and larval bullies, and seasonal changes in the size of the larval fish are shown in Figure 22. Throughout much of the year one or more of these prey items is abundant, but they are all small; _Daphnia_ up to 4 mms length, larval bullies up to ≤ 19 mms length, and larval smelt reaching a size of 25 - 30 mms by late winter/early spring.

During the period October to December 1976 inclusive,
FIGURE 22. Seasonal changes in a) the size of larval smelt (•) and larval bullies (○), and in the numbers of b) larval smelt c) larval bullies & d) Daphnia carinata (August 1976 - July 1977). Circles are the mean of 4 samples per month (2 from each station) and the vertical bars represent 95% confidence limits.
when either numbers or size of larval fish were low, Daphnia partially filled the gap in this supply of limnetic food. Terrestrial insects, particularly the Manuka beetle, Pyronota festiva, were also becoming increasingly available at the lake surface at this time.

There were two peaks in the numbers of larval fish, one in February/March 1977 and the other in June 1977.

Recruitment of juveniles to the lake

Juvenile rainbow trout entered the lake from the nursery streams mostly as autumn immigrants or spring immigrants. A high proportion of the small juvenile trout caught in the drawdown zone in April and October had retained their parr marks up to the time of capture in the gillnets, suggesting recent entry from the nursery streams. Few small juveniles were captured in the drawdown zone in February or August.

The devastating flood of New Year 1975/76 undoubtedly had a significant effect on the level of recruitment of juvenile trout to the lake during the subsequent year. The spawning streams in the northeast corner of the catchment were completely devoid of fish following the flood, but the streams rapidly recovered their invertebrate fauna, and the spawning runs of trout entered the streams as usual during the winter of 1976. The following spring electrofishing of one of these spawning streams revealed the presence of a single year class of trout (0 + fry). Their growth and seasonal timing of emigration
from the stream was followed by electrofishing at 1-2 monthly intervals, and it was established that the bulk of the autumn immigrants to the lake were the faster-growing 0+ juveniles. The slower growing 0+ juveniles overwinter in the stream and form the bulk of the spring immigrants as 1+ juveniles, (Figure 23).

This produces a bimodal length frequency distribution in the 1+ juveniles during their first year in the lake (see February 1976, and October and December 1976, Figure 23), but by the end of their second year they merge to form a single size-class.

Condition factor

The small juvenile rainbow trout have a high mean condition factor when leaving the nursery streams, but during their first 2-4 months in the lake, when they were inhabiting the drawdown zone, there was a significant drop in their mean condition factor (Figure 24). When they moved out into the limnetic zone (at a size of approximately 26 cms. length) the mean condition factor increased and remained high until they reached a size of approximately 38 cms. and then there was a gradual fall in the mean condition factor with increasing size. In "previous spawner" rainbow trout the mean condition factor was significantly lower than in immature rainbow trout of a comparable size.
FIGURE 23. Length frequency distributions of rainbow trout caught in nets during each 2 monthly sampling. * = no nets set in drawdown zone. Trout which entered the lake as juvenile immigrants in autumn = A, in spring = S. □ = immature fish with ripening gonads.
FIGURE 24. The mean condition factor of rainbow trout in relation to size and maturity (February 1976 - December 1976). (n) = sample sizes. Vertical bars represent 95% confidence limits. ○ = immature fish. × = previous spawners.
After the small juvenile rainbow trout moved out into the limnetic zone their growth rate was rapid up to a size of approximately 44 cms. There was an increase in modal length of ≈ 3 cms/month in the 1 + spring immigrant juveniles between February 1976 and June 1976, (Figure 23). Above ≈ 44 cms the growth rate slowed down.

Approximately half of the rainbow trout matured at 2 years old; the remainder continuing as immature fish into their third year are subjected to intense angling pressure in October and November, which depletes the numbers of rainbow trout maturing at 3 years old.

After reaching maturity there is little increase in length in rainbow trout, and with the fall in condition factor, very little increase in weight.
DISCUSSION

Before hydroelectric development Lake Waikaremoana was virtually a stabilized river "reservoir" of much greater age than any of the now more familiar man-made hydroelectric river reservoirs. There were natural fluctuations in lake level with a mean annual amplitude of 2.5 metres.

The morphometric changes following hydroelectric development in 1946, due to the initial lowering of the lake level, were in effect the reverse of those described before and after impoundment of the lakes of the Campbell River drainage area in B.C. (McMynn and Larkin 1953), and Loch Garry, Scotland (Campbell 1963). However, the continuing impacts may be more similar in that hydroelectric utilization of the lakes imposes a regime of lake level fluctuations, which is unnatural in periodicity, if not in amplitude as well.

MORPHOMETRIC CHANGES

The most significant morphometric changes in Lake Waikaremoana are those affecting the littoral area and the lower reaches of streams entering the lake.

The \( \leq 17\% \) reduction in the littoral area, with a disproportionately great loss of shallow littoral (\(< 5\) metres deep), will have reduced the potential total production of the littoral zone of the lake by a similar, if not greater, degree of magnitude thus diminishing both the littoral living space and
the littoral food resources for the trout to a far greater extent than the reduction in the limnetic area (≈ 4% loss). The dependence of the trout at certain stages of their life on the space and/or food resources of the littoral zone, and during certain seasons of the year, when limnetic food resources are scarce (fortunately only short, transient periods), makes the relatively small area of the littoral zone a limiting factor in the carrying capacity of the lake for trout.

Although the total length of tributary streams accessible to spawning runs of trout from the lake has been increased by the creation of gauntlets, these are of questionable value—being under the influence of lake level fluctuations (McMynn and Larkin 1953). The redds of trout spawning in the lower reaches during late winter, when lake levels are low, are liable to inundation by rising lake levels during incubation of the eggs in early spring. The sluggish flow will predispose to siltation and reduce the percolation of water through the gravels of the redds.

LAKE LEVEL FLUCTUATIONS
Seasonal periodicity

Even though there may be considerable differences in the seasonal periodicity of natural (unregulated) lakes between temperate and subarctic climates (Figure 25), following hydroelectric development they are likely to follow a similar pattern related to summer storage of water and maximum power gen-
FIGURE 25. Seasonal periodicity of natural fluctuations in lake level
a) Lake Blåsjön, subarctic Sweden (Grimås 1961)  
b) Loch Lomond, Scotland (after Slack 1957)  
c) Lake Waikaremoana  
(a & b from Elder 1975)
eration during winter (Figure 26). This will tend to produce or accentuate, a rising and maintained lake level in summer, and a falling lake level in winter.

This regulated pattern is closer to the natural periodicity of lake level fluctuations in arctic or continental climates, where winter precipitation is in the form of snowfall, and freezing temperatures delay the runoff to the lakes until the spring thaw. The delayed runoff may be prolonged into summer in high alpine and glacial melt catchments (e.g. Lillooet Lake, B.C.).

The natural fluctuations in lake level in Lake Blåsjöen following the spring runoff show a similar summer pattern to the natural fluctuations in Lake Waikaremoana - i.e. a high lake level in early summer and falling through late summer. The major difference between the natural fluctuations in these two lakes is in their winter levels - falling in Lake Blåsjöen; rising in Lake Waikaremoana.

The major change in the seasonal periodicity in Lake Blåsjöen following hydroelectric development is due to summer storage maintaining a high level throughout the summer, although this is perhaps overshadowed by the extensive increase in amplitude (Figure 26). In Lake Waikaremoana the seasonal periodicity has been totally reversed following hydroelectric development, with little change in amplitude.
FIGURE 26. The natural and regulated lake level fluctuations in Lake Blåsjön (after Grimås 1961) and in Lake Waikaremoana. The shaded areas represent the extent of submergence of the weed beds during summer. S = summer; W = winter.
Effects on light penetration and primary producers

Quennerstedt (1958) describes the effects of water level fluctuations on lake vegetation in Scandinavian lakes, and discusses the effects of summer storage. The prolonged deep submergence of the aquatic macrophyte beds during their vegetational period produces an upward displacement of the lower boundary of rooted macrophytes and also of attached algae. If a rising lake level in summer causes a reduction in water transparency as well, then this effect will be increased.

Grimås (1962) describes a reduction in water transparency due to shore erosion in Lake Blåsjön following increased water level fluctuations. In Lake Waikaremoana intense wave erosion of the papa shores accompanies a rising lake level in summer. Papa bedrock in the drawdown zone cracks and crumbles when exposed above the water level during summer. A rising lake level and wave action work upon this sunbaked papa to produce heavy papa silt loads, which are carried out into the lake in the deeper, reverse, offshore currents. Following spring and summer storms there are profound transient effects on water transparency in the littoral zones along exposed papa shores, and lesser, more prolonged effects throughout the whole lake due to wind-induced epilimnial currents. With a falling lake level the exposed papa has the texture of smooth concrete and wave action produces relatively little suspended papa silt unless extreme drawdown reaches down to the finer sediments.
of the lower drawdown zone. Shore erosion may be only partly responsible for the significant negative correlation between lake level and water transparency in Lake Waikaremoana, because there are, of course, other factors, such as suspended sediment inputs during floods and algal blooms, which reduce water transparency. Floods are associated with a rising lake level. Algal blooms, although primarily related to seasonal changes in light, temperature, and circulation of the lake, may also be associated with a rising lake level, if it is sufficient to produce a damming-up effect through flooding of terrestrial vegetation and soil (Mitchell 1975).

A rising lake level in late summer may prevent emergent species of aquatic macrophytes from penetrating the lake surface and flowering. This occurred in two out of the three summers during the study period, and may weaken any competitive advantage that these species have over Elodea canadensis. There are only female plants of Elodea in New Zealand (Fish, pers. comm.) and its growth and spread is entirely vegetative.

Winter drawdown exposes the upper littoral zone not only to dessication, but also to freezing. This commonly eliminates aquatic macrophytes from the drawdown zone (Quennerstedt 1958, Grimås 1961), but at Lake Waikaremoana, where the freezing is less severe or prolonged than in northern Scandinavia, some hardy species of native aquatic macrophytes (e.g. Myriophyllum sp.) survive. Their higher tolerance to dessication and/or
freezing gives these native species some competitive advantage over the adventive *Elodea canadensis* in the drawdown zone.

High winter lake levels provide a measure of protection to the weedbeds of the shallower littoral from the disruptive wave action of winter storms. The seasonal timing of this protection is altered by hydroelectric development.

The major cycle

The major cycle in lake level fluctuations, with its periodicity in the order of 2 - 5 years (Figure 3), will produce a shifting littoral zone. When this is showing an upward trend in the order of 1 - 2 metres depth/year (e.g. recent post-hydroelectric development period - 1970 - 1971 - Figure 5) there will tend to be an upward displacement of the lower boundary of aquatic macrophytes and a recolonization of the lower drawdown zone. Periods of extreme drawdown (e.g. winters of 1969 and 1973, Figure 4) will function as a "reset" by eliminating macrophytes in the lower drawdown zone, and if the lake level remains lower than usual during summer, by allowing some extension of macrophytes into deeper water. A complex of factors related to lake level fluctuations will affect the composition of the macrophyte beds in the drawdown zone - e.g. effects on substrate, resistance of macrophyte species to exposure, dessication and freezing, wave action, and their ability and rate of recolonization.

The major cycle combined with the altered seasonal per-
iodicity has significant impacts on the trout spawning areas in the gauntlets. During a low phase of the major cycle extensive areas of suitable gravels become available to the spawning trout. From records dating back to 1931 of the average length and weight of rainbow trout caught by anglers in Lake Waikaremoana (New Zealand Wildlife Service - unpublished data) there is evidence of fluctuations in population numbers of the rainbow trout, which seem to be correlated with the major cycle of lake level fluctuations. It appears that the amplitude and period of a "cycle" in population numbers of rainbow trout may have increased following hydroelectric development.

The rate of rise and fall in lake level

The ability of aquatic invertebrates to follow changes in lake level and avoid the danger of stranding varies with the species (Moon 1935, Hynes 1961) - and probably varies also with the time of year and water temperature.

In Lake Waikaremoana effects of lake level fluctuations on the habitat and food of littoral invertebrates (substrate, macrophytes, and attached algae) are probably more important than the dangers of stranding.

The maximum rate of drawdown in Lake Waikaremoana ($\sim 6$ cms/day) is well within the limits of the rate of drawdown (15 cms/day), which was set to provide some protection for the littoral fauna of Llyn Tegid - a hydroelectric lake in North
Wales (Hunt and Jones 1972).

LITTORAL INVERTEBRATE FAUNA

The mean number of animals per square metre immediately below the drawdown limit in Lake Waikaremoana (≤ 9000 individuals per square metre) is comparable to the density of animals in the upper 2 metres of the unregulated, northern Swedish, Lake Ankarvattnet (≤ 10,000 individuals per square metre) — see Figure 27. The samples in Lake Ankarvattnet (and Lake Blåsjön) were taken during summer and autumn (June to October inclusive) with an Ekman dredge and sieved through a 0.6 mm mesh (Grimås 1961). The 0.8 mm mesh, which was used in Lake Waikaremoana, would not have retained many of the smaller individuals counted in the Ankarvattnet and Blåsjön samples.

Water transparency in the Swedish lakes (Secchi disc readings 9.5 - 13.5 metres) was similar to Lake Waikaremoana. The thermocline, during the short period of thermal stratification (< 4 months) in the Swedish lakes occurred at a depth of approximately 3 metres, whereas in Lake Waikaremoana the thermocline lay at or below 15 metres, and this may account for the greater density of animals in the deeper littoral of Lake Waikaremoana (Figure 27). The depth of thermal stratification may therefore have a significant influence on the quantitative vulnerability of the littoral invertebrates to a given amplitude of drawdown.
FIGURE 27. The depth distribution of the bottom fauna in Lake Blåsjön and Ankarvattnet (after Grimås 1961) and in Lake Waikaremoana.
Quantitative losses

Grimås attributes the "inverted bathymetric distribution of animals" in the drawdown zone of Lake Blåsjön (Figure 27) to the effects of winter drawdown. By superimposing the Blåsjön and Ankarvattnet profiles of the quantitative depth distribution of the bottom fauna, he estimated the quantitative losses due to hydroelectric utilization of Lake Blåsjön at about 70% in the drawdown zone, and 25% below the drawdown limit.

Grimås attributes these losses in the drawdown zone to destruction of food and habitat (particularly the elimination of macrophytes), more than to direct mortality of littoral invertebrates due to stranding. Below the drawdown limit he attributes the losses to an altered temperature regime in the sediments resulting from abnormal cooling during extreme winter drawdown (an effect which extends well below the drawdown limit as deep as the upper profundal zone) and also to inorganic siltation originating from erosion in the drawdown zone, which is especially detrimental to filter-feeders such as sphaeriids.

The destruction of habitat in the shallow littoral of Lake Waikaremoana due to the smaller amplitude of winter drawdown was not as extensive, cooling of the littoral sediments is unlikely to be as extreme, but inorganic siltation from erosion in the drawdown zone may be more intense than in Lake Blåsjön. Filter feeders are not numerically prominent in the Waikaremoana littoral fauna.
Seasonal changes in depth distribution

Seasonal changes in the depth distribution of the littoral invertebrates are likely to be due to a combination of factors; differential mortality and reproductive rates between zones, seasonal migrations between zones, and for some taxa (e.g. chironomids and oligochaetes), growth to a sufficient size to be retained by a 0.8 mm mesh.

During spring and summer increasing light penetration (which would be enhanced by a falling lake level), and rising water temperatures, probably cause a bloom of attached algae in the deep littoral. The deep summer generation of *Paroxyethira tillyardi* and the summer increase in numbers of gastropods in the Nitella zone are probably associated with this. The gastropods in the Nitella zone may respond with increased reproductive rates to an increase in food supply and rising temperature, but the decrease in numbers in the mixed zone in summer is suggestive of a downward migration.

During winter the increased numbers of *Potamopyrgus antipodarum* in the mixed zone may be largely due to an upward migration. They showed a strong positive phototaxis during sorting of the live samples in late summer (March/April), which was not so apparent in *Gyraulus sp.*

The increased numbers of Odonata in the upper littoral during winter could be explained by an upward migration of late instar larvae during winter in preparation for emergence during the following spring and early summer. Macan (1977)
describes an increase in numbers in shallow water during winter of Odonata larvae in their second year.

The dragonfly, *Procordulia grayi*, emerges from late October to December. The late instar larvae are slow-moving when crawling through dense weed beds, although they can travel much faster by "jet-propulsion" across a weed-free substrate, such as the upper drawdown zone. The damselfly, *Xanthocnemis zealandica*, emerges about a month later; their final instar larvae are powerful swimmers and can rapidly traverse the weedbeds on their final emergence migration. During winter the maximum concentration of larvae of *X. zealandica* (in the mixed zone) occurs deeper than the maximum concentration of the earlier emerging, slower-moving larvae of *P. grayi* (Figure 16).

The early instar larvae of Odonata appear to be widely dispersed throughout the depth of the littoral by late summer. This probably results from the pattern of ovipositing by *P. grayi*, but for *X. zealandica* there must be some dispersal mechanism into the deeper littoral for the early instar larvae from the shallow littoral areas where the eggs are deposited. Macan (1977) describes such a dispersal of newly-hatched zygopteran larvae, which appeared to be influenced by the direction of wind-induced currents. The territorial behaviour noted previously of adult male *P. grayi* probably ensures some lateral dispersal of ovipositing in the littoral areas.

The bivalves show quite a different pattern of seasonal changes in depth distribution. Being filter-feeders they might
be expected to flourish better in a relatively weed-free sub-
strate - particularly in summer during the maximal vegetational
period of the weedbeds, but during winter the weed beds may
provide greater protection from predation. Similar ecological
requirements of the larvae of the Trichopterans, Pycnocentrodes
sp. and Paroxyethira hendersoni, may account for their similar
pattern of distribution.

Those insects, which take a single year to complete their
life cycle (e.g. Triplectides sp. and Nymphula nitens) show
a temporary decline in numbers following emergence of the
adults in summer, and before the next generation of larvae
appear.

Following hydroelectric development the rising lake level
in summer and reduced water transparency will probably reduce
the primary production of both attached algae and macrophytes
in the deeper littoral, and if the rising lake level is ex-
treme, a die-off of the deeper weed beds in summer will pro-
duce an unseasonally early detritus food chain. The signif-
icant increase in the larvae of Chironominae in the lower
Nitella zone (Figure 18), which had developed by winter 1976,
may have been related to such an event.

A rising lake level in summer may interfere with ovi-
posing by adult insects, particularly those species, such
as Xanthocnemis zealandica, which may be dependent on emergent
aquatic vegetation. Species which deposit their eggs into
shallow water may do so into an unfavourable habitat. Adult
females of *Procordulia grayi* are attracted by the dark green of underlying weed beds during ovipositing at the surface of deeper water (Armstrong 1958); the lake level during this period (December to March inclusive) may affect the distribution of their eggs in the littoral.

During the final emergence migration of final instar larvae of *Procordulia grayi* they are extremely vulnerable to predation by large trout cruising the drawdown zone. On bright sunny days (late October to December inclusive) they leave the shallower weed beds and traverse the weed-free drawdown zone to crawl out onto the lake shore. A rising lake level in summer increases the distance they have to travel across this weed free zone, increasing their availability to the trout. Tree stumps spanning the drawdown zone provide valuable escape routes from predation.

An upward migration of gastropods and the late instar larvae of *Procordulia grayi* and *Xanthocnemis zealandica* during winter would normally coincide with a rising lake level. Following hydroelectric development the falling lake level in winter, poses a greater threat of stranding, than would occur with a falling lake level in summer. *P. grayi* would appear to be particularly vulnerable in this respect (Figure 16).

**Qualitative losses**

Maximum species diversity in the littoral zone occurs in the shallow water with its greater variation in substrate and
macrophyte species. It is the shallow water fauna, which is most vulnerable to destruction by hydroelectric drawdown (Aass 1958). Fluctuating lake levels tend to produce more uniformity of substrate in the drawdown zone, as well as the elimination of some or all species of aquatic macrophytes, thus reducing the likelihood of any short term recovery of a high species diversity in this zone.

Grimås demonstrated the effects of hydroelectric development of Lake Blåsjön on the species diversity of the littoral fauna by comparison with Lake Ankarvattnet. He records 56 species of chironomids in the littoral zone of Lake Ankarvattnet and only 27 species in Lake Blåsjön. He describes a peaked and intermittent pattern of emergence of the fewer species of chironomids in Lake Blåsjön. This reduces their availability to trout as a predictable and utilizable source of food (Nilsson 1961).

The species diversity in Lake Waikaremoana may have been reduced by hydroelectric development—perhaps not so much by the amplitude of lake level fluctuations, as by some of the consequences of the altered seasonal periodicity.

New Zealand lakes, with a low species diversity anyway, can ill afford to lose even one or two species.

TROUT

Species composition

The percent composition of rainbow trout and brown trout
caught in the gillnets may not truly represent the composition in the lake. Trapping of the spawning runs of trout in the Waiotukapuna stream (one of the major spawning streams in the system) during the winters of 1971, 1972 & 1973 revealed a species composition varying from 62 to 76% brown trout (Ewing and Gibbs 1973) - compared with 18% brown trout in the netting programme (1976).

However, as the spawning runs consist only of mature fish, and the ratio of immature to mature fish in the lake differs by a factor of 4 between the species, this discrepancy can be partly accounted for. But in spite of this, the figures would suggest that rainbow trout were more vulnerable to capture in the gillnets than brown trout. Daytime observations suggest higher foraging velocities in rainbow trout than brown trout. If they remain more active than brown trout through the night, this may increase their chances of encountering a net.

Spatial segregation

The size dominance of mature brown trout over mature rainbow trout is probably of importance in interspecific interactions in the littoral zone of the lake. Both intra and inter-specific interactions in brown and rainbow trout can be clearly observed in the shallow water of the drawdown zone.

During the daytime in spring and early summer large brown trout dominate the drawdown zone. Individual fish cruise a regular beat along 50 - 100 metres of shoreline and particu-
larly during September and October aggressive encounters between brown trout can be observed, and interspecific encounters between brown trout and the occasional rainbow trout straying into the drawdown zone from the deeper littoral (a more frequent occurrence on the steeper shores). This undoubtedly hastens post spawning dispersal around the lake shore.

The significant difference in size between brown trout caught in the nets in the drawdown zone and in the deep littoral zone is probably related to daytime intraspecific interactions, and supports the direct observations of territorial behaviour and dominance of the larger fish. At nighttime, as evidenced by fly-fishing from the shore after dark, and the results of the netting programme, the rainbow trout move onto the shallows of the drawdown zone. At night they are unlikely to be affected by size-related interactions, and they showed no significant difference in size between those caught in the deep littoral zone and in the drawdown zone.

Later in summer, if surface temperatures rise to approximately 19°C, brown trout tend to leave the gently sloping shores and rainbow trout move in during the day time. Rainbow trout appear to tolerate higher temperatures. The brown trout move to cooler stream mouths or steeper shores, where they emerge from the depths and cruise a shorter beat in the drawdown zone before descending to the depths again - to reappear 15 to 20 minutes later.
A paradoxical situation has been observed in some sheltered bays where brown trout have been seen to constantly cruise the lower drawdown zone just above dense beds of *Elodea*, when water temperatures have been as high as 22°C. Photosynthetic oxygen supersaturation may raise the temperature tolerance of brown trout, if it becomes well developed in the calm waters of sheltered bays. At nighttime the brown trout may leave these warmer shallows for deeper water if the oxygen levels fall.

The behaviour of these larger brown trout has been described at some length, because the results of the netting programme (where the fish were caught at dusk, and dawn, and through the night) did not show any significant spatial segregation between brown and rainbow trout in the littoral zone of the lake - and yet direct observation during the daytime and the results of daytime angling show a very clear picture of spatial segregation during spring and early summer; the brown trout in the drawdown zone and the rainbow trout over the weedbeds of the deeper littoral.

Interactions between large brown trout and small juvenile trout in the drawdown zone have been observed, which gave a strong impression of predatory intent, but no evidence of predation by large trout on small juvenile trout was obtained. This is perhaps more likely to occur in the stream mouth gauntletts. Tilsey describes predation by brown trout on rainbow trout juveniles in Lake Eucumbene, Australia (Tilsey 1970).
Effects of hydroelectric development on available space

The lowering of the lake level in 1946 greatly reduced the area of shallow littoral, and the altered seasonal periodicity of lake level fluctuations has a profound effect on the availability of the reduced area of weed-free shallows. The length of shoreline was also reduced (≈ 10% loss - Table III).

For the larger brown trout length of shoreline is probably a more relevant spatial consideration, although the width of the weed-free shallow littoral has an important effect on the availability of food (particularly emerging dragonfly larvae). During the period of extreme drawdown the mature trout are mostly in the spawning streams. For the small juvenile trout, during their first few months in the lake, changes in this available space may be more important, and hydroelectric development may have altered the selective pressures for seasonal timing of the immigration of juvenile trout to the lake.

Even before hydroelectric development the limnetic space and food resources were probably not fully utilized by trout. The increase in ratio of limnetic : littoral areas from 5.8:1 to 6.7:1 will have accentuated the relative underutilization of the limnetic area.

Epilimnial temperatures in the lake during summer vary from year to year within approximately 2°C. above or below the critical temperature for brown trout (≈ 19°C). The depth of the thermocline is such that a cold water refuge may lie
some distance from the shore. Climatic variation from year to year undoubtedly has a more important effect than hydro-electric development on the thermal conditions in the lake, but a slight warming effect due to sealing of the shallower leaks in the dam and summer storage may have a critical effect on the brown trout during some years.

Food & condition factor

Competition for food between the small juvenile and large trout appears to be unimportant; not only are the small juveniles taking smaller food items, but it is mostly of limnetic origin, and their falling condition factor while living in the drawdown zone suggests that this supply food is either not abundant or else not consistently available. Availability of "limnetic food" in the drawdown zone probably depends upon onshore wind at night, when larval fish or Daphnia are close to the surface and liable to lateral displacement by surface currents. There is probably an erratic replenishment of this source of food to the drawdown zone, and a considerable variation between exposed and sheltered, and steep and gently sloping, littoral areas.

After the juvenile trout have moved out into the ample space of the limnetic zone with its abundant and more or less continuous supply of food the rise in their condition factor and rapid growth rate reflects the ease with which they can
fill their stomachs, but these food items are small, and when the rainbow trout reach a size of ≈ 38 cms. their condition factor starts to fall, and thereafter their growth rate declines. It is probable that at about this stage the relationship of fish size to food size (Lindström 1955) becomes critical, and the larger trout are compelled to turn more towards the limited area of the littoral zone for larger food items. Changes in condition factor in the larger trout are confounded by changes in body form associated with maturity, the ripening gonads and stresses of spawning, but the slow and incomplete recovery of condition after spawning in the rainbow trout is probably partly due to their greater dependence on the limited space and food resources of the littoral zone, and interactions with the larger brown trout.

Effects of hydroelectric development on food resources

It would be difficult to quantify the loss of production of littoral invertebrates resulting from the reduction in the area of the littoral zone, and the continuing impacts of lake level fluctuations. Littoral invertebrates make their most important direct contribution to the diet of the trout during spring, when the biomass of insect larvae and pupae is at its peak, and during early summer, when they become most available during their emergence periods. However, the importance of littoral invertebrates in food chains through bully and smelt may be more significant, and has not been studied.
The introduction of smelt has not only provided a valuable limnetic food resource, available for a longer period of the year than either larval bullies or Daphnia, but it also cycles more of the "surplus" limnetic production into the littoral areas through the onshore movement of post-larval smelt. Smelt form a greater proportion of the diet of brown trout than rainbow trout, and their introduction may therefore have benefited the brown trout more.

The gathering capacity of a lake for terrestrial insects is affected by the steepness of its shores (Norlin 1964). The lowering of the lake level with hydroelectric development and topography of the lost littoral may have reduced the availability of terrestrial insects to the trout, and this would have a greater impact on the rainbow trout. The lost littoral provides extensive areas of frog habitat, and frogs are important food items to the larger brown trout.

The effects of morphometric changes and fluctuating lake levels on the spawning of bullies and the effects of fluctuating lake levels on the spawning of smelt were not studied. Jolly (1967) describes a continuous spawning period for smelt from November to late April in Lake Taupo, and from mid-September to the end of June in Lake Rotorua. In Lake Waikaremoana the apparent gap in the recruitment of larval fish to the limnetic zone in the late summer/early winter of 1976/77 followed a period of high lake levels, suggesting that excessive summer storage may be detrimental to spawning of smelt and
perhaps also bullies. Studies of the ecology of smelt and bullies was suggested as the most useful area for continuing research at Lake Waikaremoana.

SUMMARY

1. The morphometric changes were virtually the reverse of those usually occurring with hydroelectric development of a lake, because the lake level was initially lowered rather than being raised. There was a disproportionately great loss of littoral area.

2. Fluctuating lake levels are now unnatural due more to their altered periodicity than their amplitude. The seasonal periodicity has been reversed and a "major cycle" spanning several years has been superimposed on the annual periodicity.

3. There was no initial damming-up effect, but a recurring, transient damming-up effect now occurs due to summer storage of water, the topography of the old, now grass-covered, wave-cut terraces and stream-mouth deltas, and the major cycle of lake level fluctuations.

4. Quantitative losses in the littoral invertebrate fauna can be assumed due to the reduction in the total area of the littoral. Further losses in littoral production occur as a result of lake level fluctuations, particularly due to summer submergence of the weed-beds and reduced water transparency.
5. The littoral invertebrate fauna is adapted to a falling lake level in summer, and a rising lake level in winter. Any reduction in the species diversity of the littoral fauna, which may have occurred following hydroelectric development, is likely to be related more to the altered periodicity rather than the amplitude of lake level fluctuations. New Zealand lakes with their low species diversity can ill afford to lose even a few species.

6. The small juvenile trout and old large trout are most dependent on the space and/or food resources of the littoral zone. Because of their requirements, the carrying capacity of the lake for trout has been reduced out of proportion to the reduction in the total area of the lake.

7. Rainbow trout dominate numerically, but brown trout dominate in size. Rainbow trout have probably been more adversely affected by the changes following hydroelectric development than brown trout. Brown trout appear to have benefited more from the introduction of smelt.

8. The morphometric changes in the lake are now largely of "historical" and academic interest, but fluctuating lake levels, being a continuing impact, are of more concern to Management. A more detailed understanding of the ecology of the littoral invertebrates and native fish is needed before the significance of the altered periodicity of the lake level fluctuations can be fully appreciated. However, it is probably safe to assume that any measures to restore the seasonal periodicity back
towards the natural situation would be desirable.

**MANAGEMENT IMPLICATIONS**

A country which depends largely on hydroelectric power is committed to maximum hydroelectric power generation during the winter months. The ecological impacts of a summer storage/winter drawdown seasonal periodicity in the levels of their hydroelectric lakes are unavoidable.

If there was an optimal balance between hydroelectric power and thermal (or nuclear) power, the hydroelectric power could be used more during the summer months, especially if the thermal power stations were closed down for maintenance during summer.

Thermal power stations operate most efficiently at continuous high output, and could be used to meet a greater proportion of the winter power demands. This would allow the lake level fluctuations in existing hydroelectric lakes to revert to a more natural seasonal periodicity and amplitude.

Alternatives to hydroelectric power would not only save remaining rivers and lakes from development, but could also reduce the continuing harmful impacts on already developed hydroelectric lakes and river reservoirs.
LITERATURE CITED


